ROLE OF CHARRED WOOD IN THE GERMINATION OF THE CHAPARRAL HERBS *EMMENANTHE PENDULIFLORA* (HYDROPHYLLACEAE) AND *ERIOPHYLLUM CONFERTIFLORUM* (ASTERACEAE)

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ABSTRACT

Germination of the chaparral herbs *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* is markedly stimulated by charate (powdered charred *Adenostoma fasciculatum* wood). The active component is not activated charcoal but is water soluble. Chaparral populations of *Emmenanthe* exhibit a nearly obligate dependence upon charate for germination. *Eriophyllum,* however, is facultatively dependent upon charate; charate is largely required for germination on potting soil or mature chaparral soil, but this species germinates readily on non-soil media. Soil extracts will inhibit germination of *Eriophyllum* on filter paper but this inhibition is overcome by aqueous charate extracts. Germination of this species is also reduced 50% with 0.05 M mannitol. Germination of both species is greatly stimulated by extracts of previously heated soil, though it is uncertain whether this is due to production of charate-like compounds from organic matter or to the destruction of inhibitors. Scanning electron micrographs showed that charate-stimulated germination was not accompanied by visible changes in the seed coat.

The abundant herbaceous flora characteristic of chaparral sites after fire is in striking contrast to the depauperate herb growth in mature stands. Most of the species making up this diverse "temporary" flora have seeds that remain dormant under the chaparral canopy. The mechanisms responsible for cueing germination to the postfire environment have been the subject of controversy. It has been hypothesized that allelopathic compounds leached from the shrub canopy (McPherson and Muller 1969) or produced by microbes in the soil (Kaminsky 1981) inhibit germination of native herbs and that these inhibitors are destroyed by fire. Alternatively, Christensen and Muller (1975b) and others have hypothesized that the environmental conditions under the shrub canopy are unfavorable for herb survival; thus, many species have evolved seeds that require a stimulus from fire to cue germination to the postfire environment.

Evidence in support of either of these mechanisms is relatively limited. Allelopathic inhibition of germination was demonstrated for four species in laboratory bioassays by McPherson and Muller (1969), but only with concentrations that are probably not found in

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nature (Kaminsky 1981). Christensen and Muller (1975a) did not observe allelopathic inhibition of germination for six out of eight native species. Recent experiments (following techniques of Christensen and Muller) with 28 native herb species have likewise failed to show any "allelopathic" inhibition of germination in the vast majority of species (Keeley et al. in press).

Cues from fire that might stimulate germination are intense heat and/or chemicals produced by combustion of organic matter. Sweeney (1956) applied a variety of heat treatments to seeds of many chaparral herb species but failed to demonstrate any increased germination. McPherson and Muller (1969) and Christensen and Muller (1975a) investigated the effect of heat on seed germination and found that a few species showed significantly increased germination but others did not.

Sweeney (1956) investigated whether or not chemicals from burned wood stimulated germination and he, as well as Christensen (1973), failed to observe any enhancement of germination from wood ashes. However, Wicklow (1977) and Jones and Schlesinger (1980) found that, although wood ashes produced no effect, partially charred wood produced a highly significant increase in the germination of *Emmenanthe penduliflora* Benth. (Hydrophyllaceae). A similar response has been observed for *Eriophyllum confertiflorum* (DC.) Gray (Asteraceae) (Keeley and Keeley 1982) and several other species (Keeley et al. in press).

The purpose of this study was to examine further the charred wood enhancement of seed germination in *Emmenanthe penduliflora* and *Eriophyllum confertiflorum.* Both species are locally abundant on recent chaparral burns throughout California. *Emmenanthe* is an annual that reaches its peak abundance in the first year after fire, and on some sites it may disappear by the second year. It is rare in unburned chaparral even in openings or disturbances. *Eriophyllum* is a suffrutescent perennial. Seedling establishment is largely restricted to the first post-fire year, though *Eriophyllum* seldom dominates at this time. Flowering begins in the second postfire year, and peak dominance occurs in the third or fourth years. Unlike *Emmenanthe, Eriophyllum* commonly establishes in openings within the chaparral matrix though it never is successful under the mature canopy. Specific questions addressed were: 1) Does activated charcoal stimulate germination? 2) Is the charred wood stimulatory effect due to a water soluble compound? 3) Is this effect influenced by the germination medium? 4) How is it affected by prior soil heating? 5) Do soil microbes play a role? and 6) Is charate-stimulated germination accompanied by SEM-detectable changes in the seed coat, as is the case for heat-stimulated seed germination in *Lotus salsuginosus* and other fire-type species (J. and S. Keeley, unpubl. data).

METHODS

Emmenanthe seeds were collected in 1979 from a one-year-old burn in the Santa Monica Mountains, Ventura County, California by W. Schlesinger and were from the same seed source used in Jones and Schlesinger (1980). *Eriophyllum* seeds were collected from an open site adjacent to mature chaparral in southwestern Riverside County, California in 1980. All experiments were done between July 1981 and June 1982.

Germination was compared on different media. Petri dishes (60 × 15 mm) had either 2 sheets of 5.5-cm filter paper (Whatman #42 ashless), 15 cc of vermiculite (Terra-Lite medium), acid-washed sand (J. T. Baker), potting soil (L & L UniGrow), or chaparral soil from either a mature (25 years) stand of *Adenostoma fasciculatum* or an adjacent 2-year-old burn in the San Gabriel Mountains, Los Angeles County. All three soils were filtered through a 3-mm screen. Fifty seeds were sown per dish and n = 10 dishes per treatment. Deionized water or aqueous extracts were applied (levels given in tables) and the dishes were incubated in the dark for 21 days at 5°C followed by 14 days at 23°C. This regime was repeated twice. Germination was scored every 7 days in the light.

Charate was prepared from *Adenostoma fasciculatum* stems (<20 mm dia.) by completely charring with a torch, but not ashing, and grinding in a Wiley Mill to pass a #20-mesh screen. Previous studies (S. Keeley, unpubl. data) have shown that unheated but powdered stems have no effect on seed germination. Charate treatments received 1.0 ± 0.1 g of powdered charate.

A water extract was made by soaking 2.5 g of charate in 20 ml deionized water for 18 hr and vacuum filtering through Whatman #1 ashless filter paper. Soil extracts were made as above with a ratio of 2 cc soil: 1 ml water for the potting soil and burned soil. For the mature chaparral soil the proportion of water used to prepare soil extracts was increased 30% due to much greater absorption of water by the chaparral soil. A filter paper extract was made in a ratio of 3 sheets of 9 cm #42 Whatman-ashless: 7 ml deionized water. A combined extract of charate plus soil was made by combining double strength extract of each.

Heated mature chaparral soil was prepared by spreading soil 3–4 mm deep on trays and heating to 195°C ± 5°C for 10 min. To examine the effect of microbial by-products in these soils, sterile extracts were prepared from soil 1) immediately after heating and 2) after heating, wetting and incubating for 12 days at 23°C in the dark. Sterile extracts were prepared by vacuum filtering soil extracts, prepared as described above, through sterile 0.2-μm nitrocellulose filters.

TABLE 1. GERMINATION OF *Emmenanthe penduliflora* AND *Eriophyllum confertiflorum* ON POTTING SOIL WITH CHARATE (FROM PARTIALLY CHARRED *Adenostoma fasciculatum*) OR ACTIVATED CHARCOAL. (Each dish received 7 ml H_2O; n = 10 dishes of 50 seeds each, **p < 0.01; means, within a row, with the same superscript letter are not different at the indicated significance level.)

	Percentage germination			
	Control	Charate	Activated charcoal	p
Emmenanthe	0[a]	25	0[a]	**
Eriophyllum	10[a]	57	2[a]	**

Osmolality of soil extracts was determined with a Wescor Vapor Pressure Osmometer.

Individual experiments were analyzed with one-way ANOVA on arcsin transformed data and significant differences between cell means were distinguished with Fisher's Least Significant Difference test.

Scanning electron micrographs were made of seeds to investigate effects of charate on the seed coats. Seeds were sown in petri dishes with 4.0 ml H_2O and with or without 0.5 g charate. After stratification for 21 days at 5°C, seeds were incubated at 23°C. SEM pictures were taken of a subsample of seeds each day during the first week. Seeds were dried in a critical point drier both with and without prior fixation in a glutaraldehyde and graded acetone series.

RESULTS

Table 1 compares germination of *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* in the presence of charate, made from charred *Adenostoma fasciculatum,* and in the presence of activated charcoal. Charate produced a highly significant increase in germination whereas activated charcoal did not, and therefore it apparently is not the component of charate responsible for stimulating germination.

Emmenanthe penduliflora germination on several media, with and without charate and various extracts, is shown in Table 2. Under control conditions (i.e., without charate or extracts) germination was low although across media it was significantly greater on chaparral soil. Charate significantly increased germination on all media and this charate enhancement was greatest on chaparral soil. A water extract of charate enhanced germination as well as or better than charate applied directly. Soil extracts applied to seeds on filter paper or vermiculite had no significant effect on germination.

In contrast to *Emmenanthe, Eriophyllum confertiflorum* germi-

TABLE 2. *Emmenanthe penduliflora* GERMINATION ON VARIOUS MEDIA AND TREATED WITH CHARATE AND AQUEOUS EXTRACTS OF CHARATE AND SOILS. (All dishes received 7 ml of H_2O or extract; n = 10 dishes of 50 seeds each, **p < 0.01, NS p > 0.05; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination				
	Filter paper	Vermiculite	Potting soil	Chaparral soil	p
Control	$1^{a,1}$	5^{1}	1^{a}	10	**
Charate	18^{a}	14^{a}	11^{a}	47	**
Charate extract	54	23	9	44	**
Potting soil extract	5^{1}	8^{1}	—	—	NS
Chaparral soil extract	6^{1}	4^{1}	—	—	NS
p	**	**	**	**	

nation under control conditions was substantially greater on filter paper than other media (Table 3). This relatively high germination on filter paper (without charate) was significantly reduced with the addition of soil extracts. Charate significantly enhanced germination on all media, though a water extract of charate significantly enhanced germination only on filter paper and vermiculite.

Some of the treatments used with *Emmenanthe* (Table 2) were replicated with less moisture on filter paper, and higher moisture on other media (Table 4). Under control conditions (without charate or extracts) the additional moisture resulted in higher germination on potting soil than on chaparral soil, a reversal of the pattern observed in Table 2. From a comparison of the same media treatments in Tables 2 and 4, it is clear that altering the moisture levels can greatly magnify the charate response. Of particular interest is the observation that chaparral soil heated and cooled prior to sowing produced relatively high germination without charate. Equally surprising was the observation that neither charate nor charate extract enhanced germination on this previously heated soil.

Some of the media treatments used with *Eriophyllum* (Table 3) were also replicated with different moisture regimes (Table 5). These experiments show that once again even without charate *Eriophyllum* seeds germinate readily on filter paper but less so on other media, in particular on soils. Addition of filter paper extract reduced germination on filter paper but had no effect on soils, whereas on sand it produced a response comparable to the charate effect. In Table 3 it was noted that soil extracts reduced germination on filter paper and vermiculite. However, these soil extracts do not inhibit germination when combined with charate extract (Table 5). Heated soil extract increased germination on all media except filter paper.

An examination of the effect of different osmotic pressures on

TABLE 3. *Eriophyllum confertiflorum* GERMINATION ON VARIOUS MEDIA AND IN COMBINATION WITH AQUEOUS EXTRACTS OF CHARATE AND SOILS. (All dishes received 7 ml of H_2O or extract; n = 10 dishes of 50 seeds each, **p < 0.01; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination				
	Filter paper	Vermic-ulite	Potting soil	Chap-arral soil	p
Control	28	$7^{a,1}$	$6^{a,1}$	$2^{a,1}$	**
Charate	55^{a}	$64^{a,2}$	56^{a}	37	**
Charate extract	70	59^{2}	$12^{a,1}$	$9^{a,1}$	**
Potting soil extract	7^{1}	1^{1}	—	—	**
Chaparral soil extract	13^{1}	2^{1}	—	—	**
p	**	**	**	**	

germination was done for species in the absence of charate. In these experiments 9 ml of water or mannitol were the only media in the petri dishes. *Emmenanthe* did not germinate under any of these conditions. *Eriophyllum* germination was 34% with water, 18% and 0% with 0.05 M and 0.15 M mannitol respectively ($p < 0.01$, LSD = 6, n = 10 dishes of 50 seeds each). Several conclusions can be drawn from these experiments. Previous tables (3 and 5) showed, under control conditions (i.e., without charate or extracts), higher *Eriophyllum* germination on filter paper than on other media. In the present experiments 34% germination with just water but no filter paper suggests there is no effect due to filter paper per se. Germination however is strongly influenced by the osmotic pressure of the medium. At 0.05 M germination was reduced 50%, possibly explaining some of the reduced germination observed with soil extracts (Tables 3 and 5), which had osmolalities between 0.04–0.05 M.

Germination of both species on mature chaparral soil and on 2-year-old-burn soil, both with and without prior soil heating, is shown in Table 6. On mature chaparral soil both species showed greatly enhanced germination when the soil was previously heated. Sterile extracts made from this heated soil produced comparable germination to the heated soil itself. However, for both species, if the soil was wetted and incubated before the sterile extract was prepared, there was a significant reduction in germination. On burn soil, germination was greater than on mature soil for both species and heating the soil prior to sowing produced higher germination. Both species showed the highest germination with sterile extracts from heated burn soil. However, if this heated soil was incubated prior to making sterile extracts, germination was reduced only for *Emmenanthe*.

For both species, SEM pictures failed to show any differences in

TABLE 4. *Emmenanthe penduliflora* GERMINATION ON ADDITIONAL MEDIA AND IN COMBINATION WITH CHARATE AND AN AQUEOUS EXTRACT OF CHARATE. (Moisture levels differed from Table 2; filter paper dishes received 4.5 ml and all other dishes received 9 ml of H_2O or extract; n = 10 dishes of 50 seeds each, **p < 0.01; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination						
	Filter paper	Vermic-ulite	Sand	Potting soil	Chap-arral soil	Heated chapar-ral soil (195°C 10 min)	p
Control	0^{a}	$9^{a,b}$	2^{a}	$15^{b,c}$	1^{a}	27^{c}	**
Charate	$73^{a,1}$	$54^{b,c,1}$	$64^{a,b,1}$	$60^{a,b,1}$	47^{c}	25	**
Charate extract	87^{1}	$64^{a,1}$	$46^{a,b,1}$	$53^{a,b,1}$	15^{c}	$34^{b,c}$	**
p	**	**	**	**	**	NS	

seed coats between ungerminated controls and germinated charate treated seeds.

DISCUSSION

On soil, germination of the majority of *Emmenanthe penduliflora* and *Eriophyllum confertiflorum* seeds is stimulated by a water soluble extract of charred wood. The difference in response observed for these two species on other media suggests that the mechanism of charate stimulation may differ.

Germination under control conditions (i.e., in the absence of charate or other extracts) is distinctly different between these two species. Without charate, *Emmenanthe* germination is always very low but is consistently lower on filter paper than on soils (Wicklow 1977, Jones and Schlesinger 1980; Tables 2 and 4). *Eriophyllum* shows consistently higher control germination on non-soil media, and on certain media, germination may be as high for controls as for charate treatments on soil. It is clear that whatever is in soils that reduces *Eriophyllum* germination, it is water soluble because aqueous soil extracts applied on filter paper reduced germination to levels observed on soils.

Charate consistently enhances germination for both species regardless of media, though the magnitude of charate-stimulated germination varies with medium and moisture level. Wicklow (1977) found that *Emmenanthe* germination with charred wood was highest on potting soil and lowest on filter paper, whereas Jones and Schlesinger (1980) reported highest on filter paper and lowest on chaparral soil. In the present study *Emmenanthe* germination in the presence

TABLE 5. *Eriophyllum confertiflorum* GERMINATION ON ADDITIONAL MEDIA AND IN COMBINATION WITH VARIOUS EXTRACTS. (Moisture levels differed from Table 3; filter paper dishes received 4.5 ml and all other dishes received 9 ml of H_2O or extract; n = 10 dishes of 50 seeds each, **p < 0.01, NS p > 0.05; means, within a row, with the same superscript letter and, within a column, with the same superscript number, are not different at the indicated significance level.)

	Percentage germination						
	Filter paper	Vermic-ulite	Sand	Potting soil	Chap-arral soil	Heated chapar-ral soil (195°C 10 min)	p
Control	62[1]	26[a,1]	27[a]	12[b]	8[b]	35	**
Filter paper extract	49[2]	26[1]	64[1]	14[a]	7[a]	—	**
Charate extract	75[a,3]	70[a,2]	62[1]	—	—	—	**
Charate extract & potting soil extract	66[a,1]	68[a,2]	53[1]	—	—	—	**
Charate extract & chaparral soil extract	73[1,3]	72[2]	53[1]	—	—	—	NS
Heated chaparral soil extract	49[2]	39	77[1]	—	—	—	**
p	**	**	**	NS	NS		

of charate was highest on chaparral soil and lowest on potting soil in one experiment and in another experiment highest on filter paper and lowest on chaparral soil. The only parameter that varied in these two experiments was moisture level which suggests that slight differences in experimental conditions can produce subtle differences in germination.

For both species germination was higher on soil from a two-year-old burned chaparral stand. This likely derives from residual charred wood remains in the soil. The consistently higher germination for both species on both soils when the soil was heated (but cooled prior to sowing) is possibly due to the production of a stimulant similar to what is produced in charred wood. Several observations support this. It is already known that wood need not be charred to stimulate germination: *Adenostoma* wood heated to 175°C for 10 min and powdered, produces significantly greater germination for both of these species over unheated powdered wood (S. Keeley, unpubl. data). It is also known that both heated lignin and cellulose are responsible for this effect (S. Keeley, unpubl. data). Thus plant litter in the soils, upon heating, may contribute to the stimulation of germination observed for both species (Table 6). That the propor-

TABLE 6. GERMINATION OF *Emmenanthe penduliflora* AND *Eriophyllum confertiflorum* ON MATURE AND BURNED CHAPARRAL SOILS WITH OR WITHOUT PRIOR HEATING OF THE SOIL (WITH 9 ml H_2O). In addition, sterile extracts of these heated soils were made, either immediately after heating or following wetting and incubating at 23°C for 12 days (4.5 ml of sterile extract were applied to petri dishes without other media; n = 10 dishes of 50 seeds each, **p < 0.01, NS p > 0.05; means, within a row with the same superscript letter are not different at the indicated significance level).

	Percentage germination				
			Sterile extract of heated soil		
	Control (not heated)	Soil heated (195°C 10 min)	No incubation	Prior incubation	p
Emmenanthe					
Mature chaparral soil	0	31[a]	32[a]	1	**
Burned chaparral soil	6	17	74	24	**
p	**	**	**	**	
Eriophyllum					
Mature chaparral soil	9	48	58	28	**
Burned chaparral soil	28	52	72[a]	68[a]	**
p	**	NS	**	**	

tional increase was always greater when soil from mature chaparral (with greater plant matter) was heated is consistent with this hypothesis.

An inevitable complication in experiments using natural substrates is the interaction with microbes. This could have been a complicating factor in our experiments with natural soils. As mentioned above, heated soils stimulate germination of *Emmenanthe* and *Eriophyllum*. However, if these heated soils are incubated under conditions suitable for microbial growth, a sterile extract of this soil will inhibit germination over a sterile extract made immediately after soil heating (Table 6). Whether or not microbial toxins control germination of these species under natural conditions is unknown. Kaminsky (1981) has argued that dormancy of chaparral seeds under the mature canopy is due to just such an effect. The fact that *Emmenanthe* does not germinate in mature chaparral soil is not likely because of such toxins since it will not germinate on filter paper or other artificial substrates unless charate is applied. *Eriophyllum* seeds appear to be inhibited by natural soils, thus it is possible that microbes play a role in limiting its germination in mature chaparral.

Two mechanisms of charate-stimulated germination may be operating in these two species, though presently it is not possible to attribute conclusively one or the other to either species. 1) Charate may "bind" or deactivate an inhibitor in the soil and thus release

seeds from inhibition or 2) charate may act directly on the seed either by extracting or altering an inhibitor, affecting seed coat membrane permeability or directly stimulating germination in some other way.

Chaparral populations of *Emmenanthe penduliflora* (but not desert populations, e.g., Jones and Schlesinger 1980) show a nearly obligatory dependence upon charate for germination, regardless of the medium, and thus mechanism number one seems unlikely.

Eriophyllum confertiflorum shows a facultative response to charate in that germination is most dependent upon charate when seeds are sown in soil. However, the data presented here for *Eriophyllum* are consistent with either of the two mechanisms proposed above. Consistent with mechanism number one are the following: germination without charate is consistently much higher on non-soil media, soil extracts inhibit germination and charate extract overcomes inhibition due to soil extracts. However, mechanism number two can not be ruled out for several reasons. One is that charate increases germination on both soils and artificial media. Higher germination on artificial media in the absence of charate can be explained as the result of an inhibitor within the *Eriophyllum* seed that is easily leached out in deionized water but not in soil solutions with their higher osmotic pressures. Observations consistent with this interpretation are: the strong inhibition of germination by mannitol, the reduction of germination on filter paper with the addition of soil extracts and even with the addition of filter paper extract.

Emmenanthe penduliflora and *Eriophyllum confertiflorum* seedlings are abundant in recently burned chaparral stands. Previous studies have shown that heat per se has no stimulatory effect on germination of either species (Sweeney 1956, Keeley and Keeley 1982, Keeley et al. in press). On the natural soils the bulk of the seed pool of each species requires contact with a water soluble product from charred wood. This product is presumably most abundant immediately after fire, as is germination of *Emmenanthe* and *Eriophyllum*. With time, charred fragments are very likely leached of this product accounting for the reduced establishment of these species in older burns. This may account for the distribution of annual species such as *Emmenanthe penduliflora* (and other charate dependent species such as *Phacelia* spp.) in older burns. In the first year after fire these herbs are locally widespread, but in subsequent years the few that are present are commonly clumped around the charred remains of shrubs (J. and S. Keeley, pers. observ.). Eventually another fire will be required for additional seedling establishment.

Perennial species such as *Eriophyllum confertiflorum* dominate burned sites for several years after fire, though largely from seedlings

established the first year after fire (Keeley et al. 1981). *Eriophyllum* germination is much more dependent upon charred wood on soils than on artificial media, suggesting that at least for part of the seed pool, the charred wood product may overcome some inhibitory component of soils. As the shrub canopy returns, the bulk of the seed pool remains dormant until the next fire. However, away from the shrub canopy, soils apparently are less inhibitory since *Eriophyllum* (unlike *Emmenanthe*) commonly establishes in gaps within the chaparral matrix.

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